

MANTLE CANAL PATTERNS IN *SCHIZOPHORIA* (BRACHIOPODA) FROM THE LOWER CARBONIFEROUS OF NEW SOUTH WALES

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ABSTRACT. The brachiopod *Schizophoria verulamensis* Cvancara, from the Lower Carboniferous of the Gresford district, New South Wales, has distinctive mantle canal patterns in small, medium, and large specimens. The different patterns are interpreted as stages in the ontogeny and are thought to result mainly from the growth and enlargement of the genitalia.

Changes in the morphology of the canals in pedicle valves throughout six horizons in the Lower Carboniferous sequence show a trend, probably genetically controlled, towards the earlier maturity of the genitalia. The superimposition of larger or mature mantle canal systems on smaller or immature systems indicates that the canals are impressed by periodic resorption, and it is argued that this probably took place during the winter when there was a stable mantle canal system and little shell deposition. In large specimens there are connexions between the vascula genitalia, vascula media, and lateral canals in the pedicle valve, and between the vascula genitalia and vascula myaria in the brachial valve. It is suggested that the connexions may have increased the amount of oxygenated coelomic fluid circulating over the gonads, possibly causing them to ripen earlier.

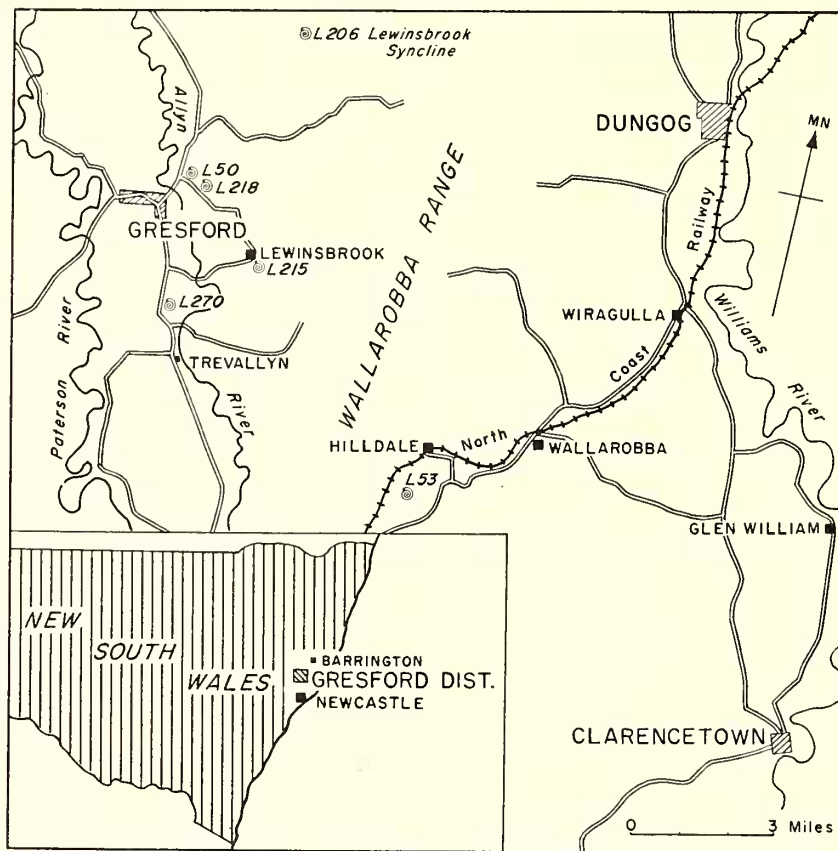
Pathological variations in the mantle canals are described, and it is shown that the canals are able to adjust to injuries or defects in the shell.

THE mantle canals in living brachiopods are extensions of the body cavity into the mantle. Their function is mainly respiratory and in articulates they also act as receptacles for the gonads. In both living and fossil brachiopods the pattern of canals is frequently impressed on the inner surface of the shell, particularly that of older specimens. In fossil brachiopods impressions of the mantle canals are common in orthoids and strophomenoids, are rarely seen in the spiriferoids and chonetoids, and only recently have been observed in two species of productoids from the Lower Carboniferous of the Bonaparte Gulf Basin, northwestern Australia. As a result their use in systematics is limited.

Schuchert and Cooper (1932) described the morphology of the mantle canals in the orthoids and used the canal patterns as a basis for the separation of a new subfamily. Öpik (1934) further demonstrated their use in his study of the Clitambonitidina, and proposed a detailed terminology for the various parts of the mantle canal system. Williams (1956) was the first to present a comprehensive review of the mantle canal patterns in articulate brachiopods. He modified Öpik's terminology and showed that the mantle canal patterns in articulates could be referred to standard types which were probably derived from Cambrian forms. Williams (1956) and Williams and Rowell (1965) illustrated many different types of mantle canal patterns.

The present study deals with the morphology, development, and probable genetic changes in the mantle canals of the Lower Carboniferous orthoid *Schizophoria verulamensis* Cvancara (1958). Extremely well-preserved material has made possible the recognition of a sequence of young, mature, and old stages in the mantle canal system of *S. verulamensis*. These stages have in turn led to the recognition of a trend towards an earlier maturity of the reproductive system during the Lower Carboniferous, and a

method of impression or superimposition of the mantle canals which had not previously been recognised in the Brachiopoda. Because of the exceptionally fine preservation it has also been possible to recognize an intricate interconnexion between the various parts of the mantle canal system, a feature not recognized in Williams's and Rowell's treatment of mantle canal patterns.



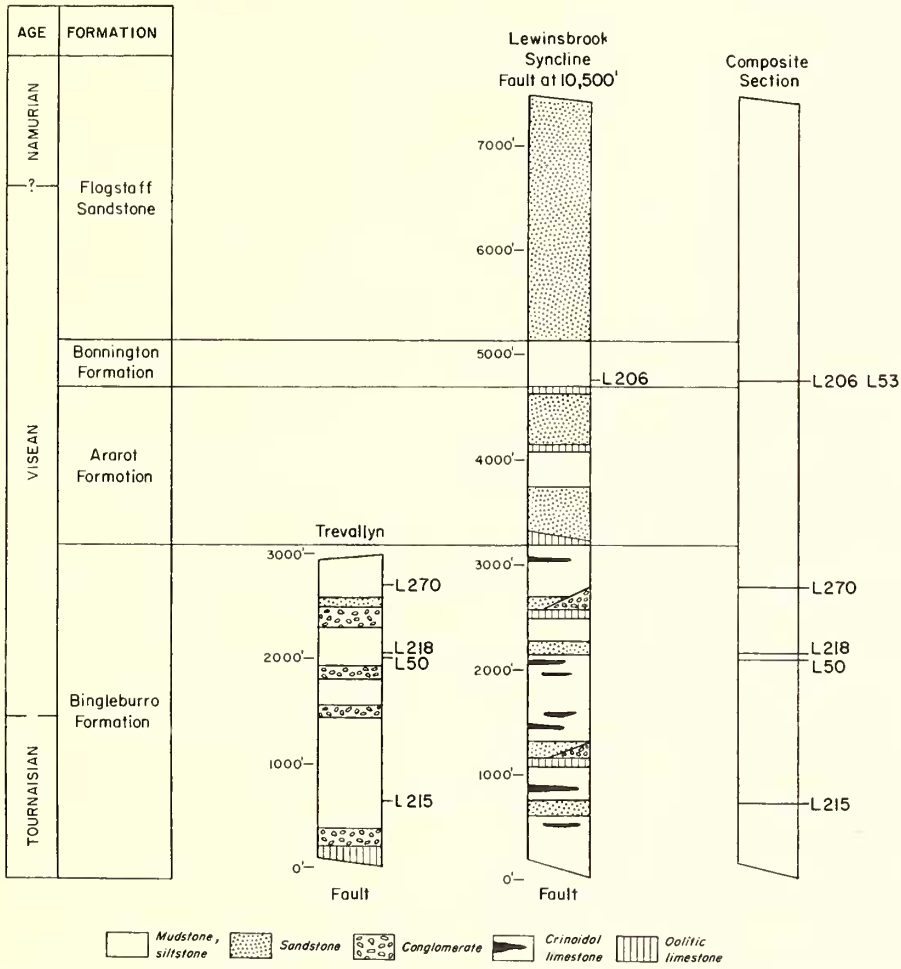
TEXT-FIG. 1. Locality of the Gresford District, N.S.W.

Schizophoria verulamensis Cvancara is one of the most common brachiopods in the Lower Carboniferous (Tournaisian and Viséan) of New South Wales, and has been collected from every known fossil horizon in the Gresford district, about 35 miles north-west of Newcastle (text-fig. 1). The majority of the specimens described in this paper are preserved in indurated grey siltstone; the rest occur in medium-grained lithic sandstone. They are exceptionally well preserved, and have very finely detailed impressions of the mantle canals and setal follicles. Internal moulds only are figured in the plates because the impressions of the canals, represented by ridges, are particularly prominent when illuminated by an oblique light source.

Schizophoria verulamensis is especially well represented in collections from the following localities (with grid references): L. 53 Greenhills (46609790), L. 206 Lewins-

brook syncline (46279968), L. 270 Trevallyn (45729864), L. 218 Gresford Quarry (45809912), L. 50 Gresford Quarry (45789913), L. 215 Lewinsbrook (46089882).

With the exception of L. 53 Greenhills, which is on the Paterson One-Mile Sheet, the grid references are taken from the Dungog One-Mile Sheet. The stratigraphic positions



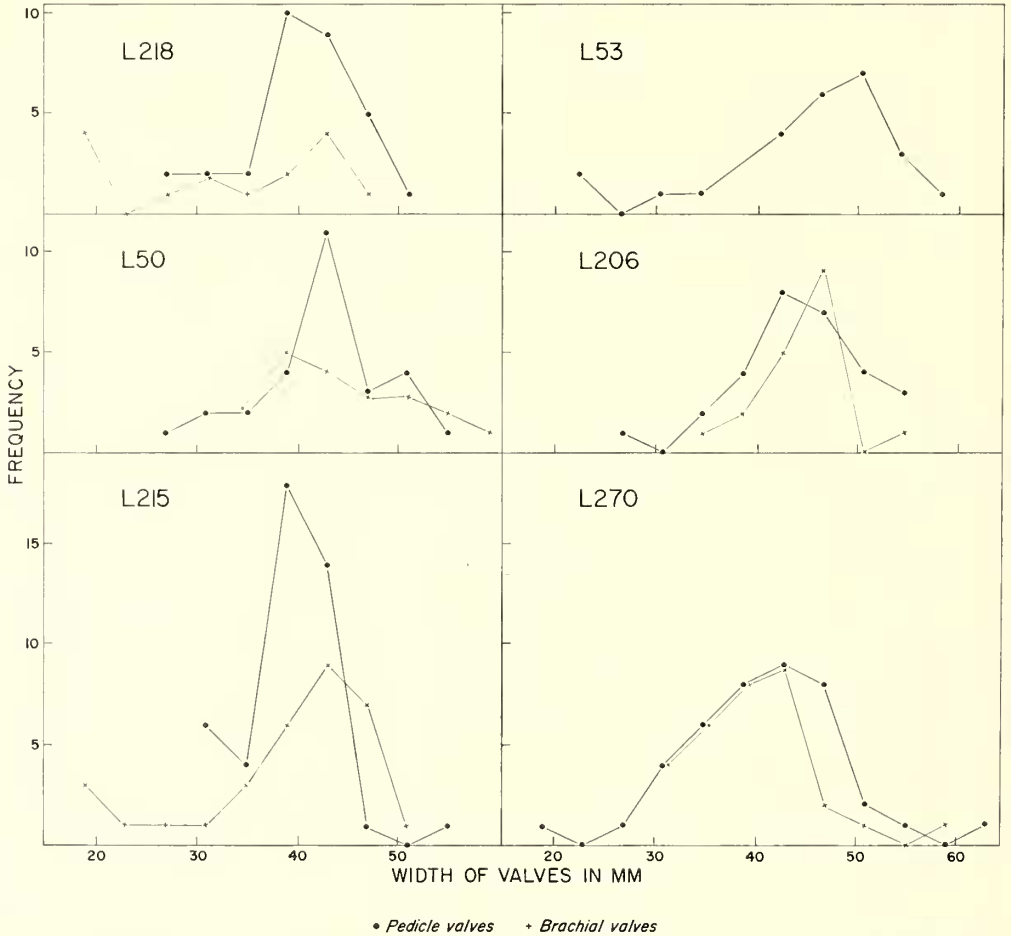
TEXT-FIG. 2. Diagrammatic stratigraphic sections of the marine rocks at Trevallyn and in the Lewinsbrook Syncline.

of the horizons are shown in text-fig. 2 on diagrammatic stratigraphic sections of the marine rocks in the north-western part of the Gresford district. All of the collections are housed in the Geology Department, University of New England, Armidale, N.S.W.

The stratigraphy of the Gresford district has been described by Roberts (1961 and 1965c) and the faunas by Roberts (1963, 1964, and 1965a and b), Campbell and Roberts (1964), and Brown, Campbell, and Roberts (1965).

The specimens of *Schizophoria verulamensis* were collected from a single horizon at each fossil locality except L. 53, where two horizons were sampled. An attempt was

made to collect randomly at each locality, and all the specimens collected were examined in the laboratory. Width-frequency plots for pedicle and brachial valves are given in text-fig. 3. The samples are characterized by the almost total absence of small specimens, and the presence of a large number of disarticulated valves, features which suggest that the populations had been affected by current action and sorting prior to burial.



TEXT-FIG. 3. Width-frequency polygons for *Schizophoria verulamensis* Cvancara specimens from six localities in the Gresford district.

The post-mortem modification is also borne out by the unequal numbers of pedicle and brachial valves and small number of articulated shells collected from each locality. These figures are given in Table 1. The collection from L. 270 is the only sample having a comparable number of pedicle and brachial valves and also contains the greatest number of articulated shells, suggesting that it is perhaps the closest to a life assemblage.

Further evidence that most of the assemblages are death assemblages is provided by the occurrence, at L. 218, L. 270, and L. 206, of shell beds containing large numbers of

mature specimens of *Schizophoria* to the virtual exclusion of smaller specimens and other small species. The L. 53 horizon contains several other large species as well as *Schizophoria*, but also has very few small species. Smaller species and polyzoan debris accompany the *Schizophoria* specimens at L. 215 and L. 50.

TABLE 1

Locality	Disarticulated valves		Articulated shells
	Pedicle valve	Brachial valve	
L. 53	25	6	—
L. 206	28	18	1
L. 270	31	30	10
L. 218	30	23	1
L. 50	25	20	5
L. 215	54	31	7

MANTLE CANALS

The mantle canals in living brachiopods are situated in the mesenchyme layer of the mantle and are lined with ciliated epithelium. They are filled with coelomic fluid, which is rapidly circulated by the ciliated epithelium (Hyman 1959, p. 593), the circulation in some species being facilitated by a median ridge dividing the in- and out-flowing currents. The coelomic fluid contains free coelomocytes, including a spherical type which has a respiratory function and may be equivalent to a red blood corpuscle (Hyman 1959, p. 557). The pigment in the 'respiratory cells' absorbs oxygen and on reduction releases it to oxygenate the tissues.

The pattern of the mantle canals varies in different brachiopod groups (Williams 1956), and there is usually a different pattern in the pedicle and brachial valves. In most cases the canals originate as wide branches from the body cavity; some of these divide repeatedly until they extend to the proximal ends of the setal follicles around the edge of the mantle; other form sac-like receptacles and act as gonocoeles.

Most living brachiopods have a complicated system of mantle canals extending throughout the mantle, providing a large surface area through which oxygenation of the coelomic fluid can take place. An adaptation to increase the surface area of the mantle canals is illustrated by Williams and Rowell (1965, fig. 24) in which the mantle canals in the inarticulate *Glottidia* subtend gill ampullae into the mantle cavity.

In some fossil groups, however, the mantle canals have a relatively small surface area, and respiration may have been largely carried out by the lophophore. The lophophore in modern articulates has a plentiful supply of coelomic fluid provided by the coelomic canal and the small brachial canal (Williams and Rowell 1965, fig. 30). The small brachial canal gives off a branch to each of the filaments on the lophophore which have a large surface area and are ideally suited to respiration. Spiriferoids, for example, had narrow pinnate mantle canals with a small surface area combined with a large spiral lophophore. The lophophore probably had a large surface area suitable for oxygen exchange, was bathed in a stream of fresh water brought in by the moving filaments, and was an ideal organ for respiration as well as food gathering. Mantle canals appear to be poorly developed in the productoids, which probably also had a spiral lophophore

(Williams 1956, fig. 5 (6); Brunton 1966, figs. 8 and 9), and the lophophore may have acted as the main respiratory organ. Chonetoids occasionally exhibit mantle canals (Muir-Wood 1962, pl. 6, fig. 7), but they too probably used a spiral lophophore for respiration as well as for food gathering.

The mantle canals are also the receptacles for the gonads in living articulate brachiopods, and so the gonads are continuously bathed in oxygenated coelomic fluid.

Blood vessels, which are distinct from the mantle canals, extend from the body cavity into the mantle canals and run along the margins nearest the mantle cavity (i.e. along the inner margins of the mantle canals). These vessels, which are only seen in living brachiopods, follow all the branches of the mantle canals and extend to the margin of the mantle, and also form anastomosing blood sinuses to the gonads (Hancock 1859, pl. 55, fig. 1; pl. 63, fig. 1; and pl. 56, fig. 4). The blood system in brachiopods is an open system, the blood returning to the body cavity by way of tissue spaces. The blood itself is generally free of cells (Hyman 1959, p. 558) and consists of a colourless lymph-like fluid. Because the blood seeps back to the coelomic cavity before being recirculated it is probably coelomic fluid from which the coelomocytes have been filtered off. The blood system is responsible for the supply of nutriment to the organs within the body cavity, the gonads, and to the mantle, especially to the cells at the growing edge of the mantle. Waste products are probably transported by the blood as it filters through the tissues back to the coelome, where they are removed by the nephridia. The blood must also contain dissolved minerals, mainly calcium carbonate, for deposition as shell material by the cells at the growing edge of the mantle.

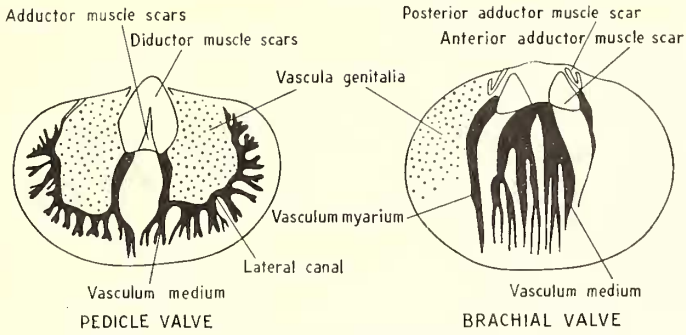
MANTLE CANALS IN *SCHIZOPHORIA VERULAMENSIS*

The morphology of the mantle canal impressions in both valves of *Schizophoria verulamensis* is shown in text-fig. 4. In the following description of the mantle canal system I propose to use the term 'canals' for the impressions of the mantle canals on the inner surfaces of the valves so as to avoid another descriptive term.

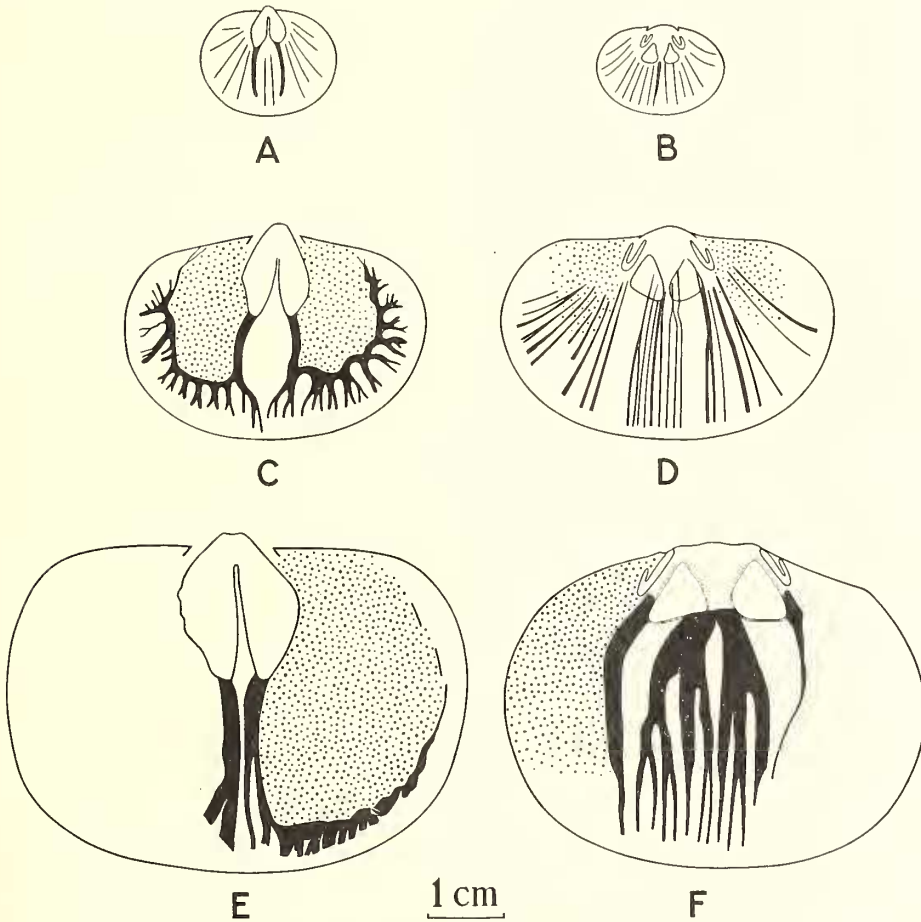
The mantle canals of small and apparently sexually immature specimens of *Schizophoria verulamensis* consist of small canals of *vascula media* and *vascula myaria* as well as a large number of narrower linear canals originating from the anterior and antero-lateral margins of the muscle field and extending to the margins of the valve (text-fig. 5 *a, b*). There is no differentiation of *vascula genitalia*.

In the pedicle valve the impressions of the *vascula media* arise from the anterior margins of the diductor muscle scars and extend with only minor branching to the front of the valve. An arcuate lateral canal such as that in older individuals (text-fig. 5*c*) does not appear to have been developed and the lateral margins of the valve were presumably supplied with coelomic fluid by the narrow linear canals extending from the body cavity.

Impressions of the mantle canals are less frequently preserved in brachial valves. Small brachial valves have canals of *vascula media* originating from between the inner margins of the anterior adductor muscle scars or, more rarely, from the inner parts of the adductor scars, and extending towards the front of the valve. The *vascula myaria* are simple, straight canals arising from between the anterior and posterior adductor muscle scars and extending towards the postero-lateral margins.



TEXT-FIG. 4. Morphology of the mantle canal impressions in *Schizophoria verulamensis* Cvancara.



TEXT-FIG. 5. Mantle canal patterns in *Schizophoria verulamensis* Cvancara showing the development from small to large individuals. The pedicle valve is on the left and the brachial valve on the right.

Larger, apparently sexually mature individuals (text-fig. 5 *c, d*) have an interconnected system of vascula genitalia in the pedicle valve (Pl. 74, fig. 3), an incipient system of vascula genitalia in the brachial valve (Pl. 74, fig. 6), and more complex vascula media and vascula myaria canals.

In the pedicle valve of mature individuals the main canals of vascula media are well separated from one another and are much broader and more deeply impressed than in the younger form. Each of the main canals branches distally, giving off a number of canals which run to the front of the valve, and an arcuate lateral canal which extends parallel with the margin of the valve to the hinge. The lateral canal has a crenulate pattern and at the peak of each crenulation gives off a major branch, which usually subdivides several times before reaching the margin of the valve. Towards the hinge the lateral canal is irregularly crenulate and terminates in a group of diverse branches. The vascula genitalia cover an area enclosed by the muscle field, the vascula media, and the inner margins of the arcuate lateral canals, and are connected by numerous branches with the vascula media and lateral canals; the significance of these connexions will be dealt with below.

The vascula genitalia in brachial valves having the same size and presumably the same age as mature pedicle valves do not appear to be as strongly impressed as those in the pedicle valve. The genital markings consist of pit-like depressions or incipient interconnected canals on the postero-median parts of the valve, and give rise to numerous branching canals, similar to those of the vascula media and vascula myaria, which extend to the lateral margins (Pl. 74, fig. 6). There are up to ten canals of vascula media, and ten canals of vascula myaria extending with variable bifurcation towards the anterior margin. Both the vascula media and vascula myaria leave tracks on the anterior adductor muscle scars.

In the largest and probably gerontic specimens (text-fig. 5 *e, f*) the mantle canal system is frequently more strongly impressed on the inner surface of the shell and is characterized by even broader main canals and an expansion of the vascula genitalia.

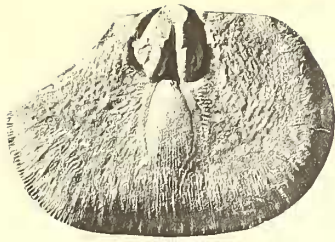
EXPLANATION OF PLATE 74

Schizophoria verulamensis Cvcancara

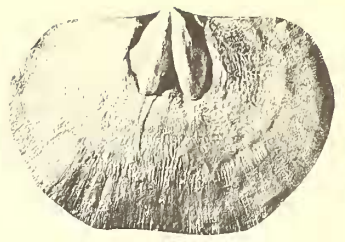
- Fig. 1. $\times 1$. F.7145a. Internal mould of pedicle valve showing the connexions between the vascula media and vascula genitalia; L. 215 Lewinsbrook.
- Fig. 2. $\times 1$. F.7145r. Internal mould of pedicle valve; note the truncation of the narrow canals by the main canals of vascula media; L. 270 Trevallyn.
- Fig. 3. $\times 2$. F.4677a. Internal mould of pedicle valve showing a sexually mature mantle canal system superimposed over an immature system; L. 215 Lewinsbrook.
- Fig. 4. $\times 1$. F.8036. Internal mould of pedicle valve showing a third canal of vascula media extending to the front of the valve; L. 50 Gresford Quarry.
- Fig. 5. $\times 1$. F.7147q. Internal mould of brachial valve showing a sexually immature pattern of narrow linear mantle canals; L. 270 Trevallyn.
- Fig. 6. $\times 1$. F.7141a. Internal mould of brachial valve showing the early development of the vascula genitalia; L. 215 Lewinsbrook.
- Fig. 7. $\times 1$. F.7153b. Internal mould of mature brachial valve showing the connexion between the vascula genitalia and the vascula myaria; L. 50 Gresford Quarry.
- Fig. 8. $\times 1$. F.7153c. Internal mould of a mature brachial valve; note the connexion between the vascula genitalia and the vascula myaria; L. 50 Gresford Quarry.
- Fig. 9. $\times 2$. F.7153a. Internal mould of an old brachial valve; note the narrow canals emerging from beneath the wide superimposed canals of vascula media; L. 50 Gresford Quarry.



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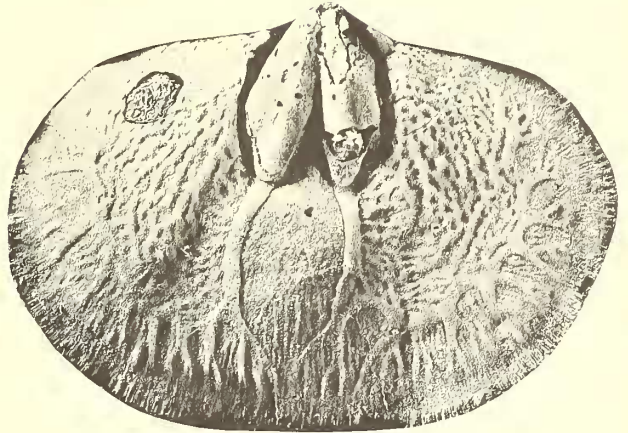
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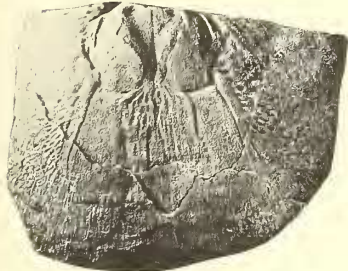
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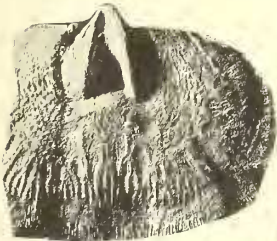
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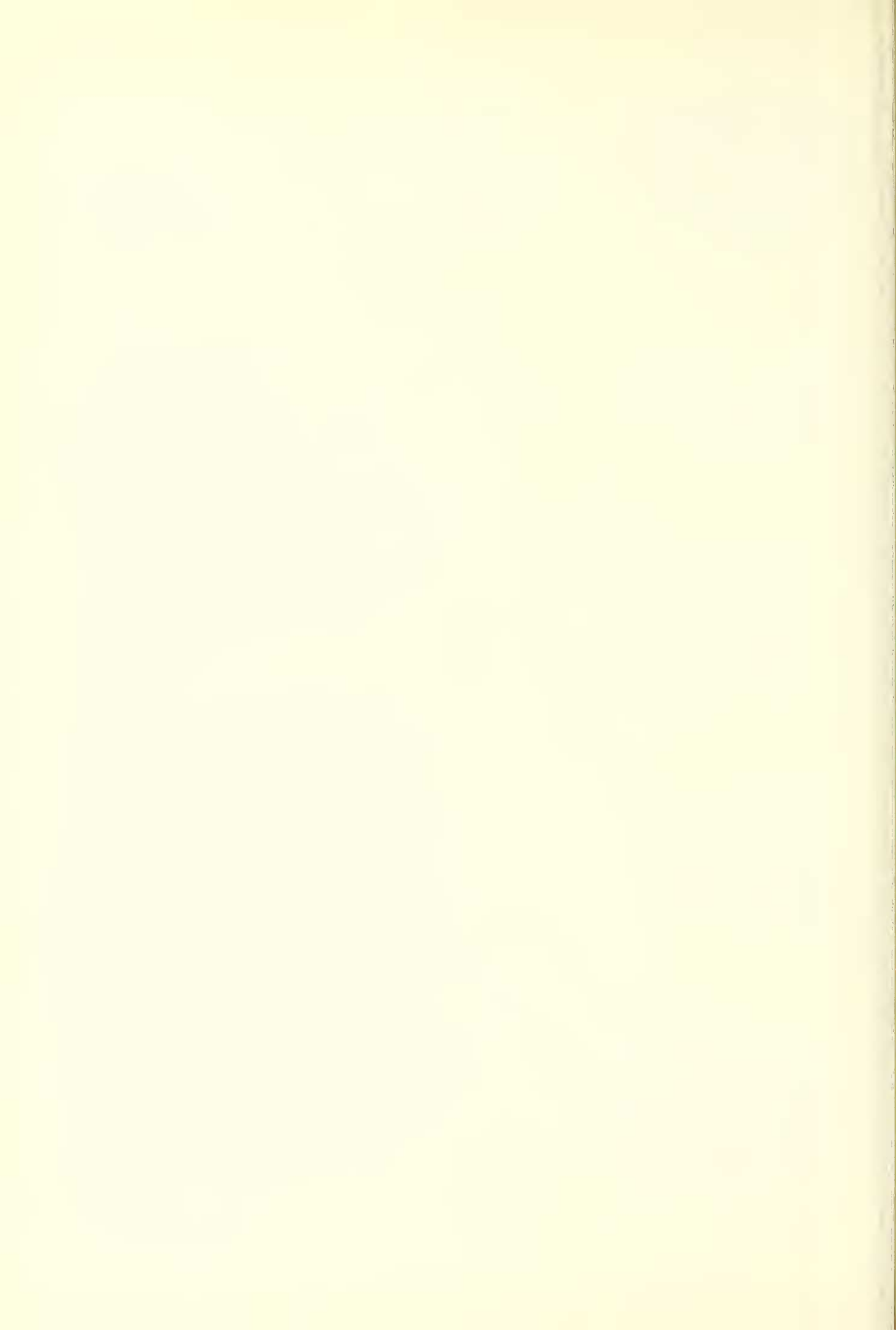
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In the pedicle valve the main vascula media canals are close together and branch distally, the arcuate lateral canals are closer to the margin than in younger specimens, and the vascula genitalia have the same ramifying canals as those in mature specimens, covering almost the entire inner surface of the valve (Pl. 75, figs. 4–7).

The canals of vascula media in the brachial valve are usually wider than in smaller specimens but do not appear to have significantly altered their positions. The vascula myaria are also broader and run straight to the antero-lateral margins, or are bent inwards at their distal extremities. Many small branches along the outer margins of the vascula myaria provide a connexion with the vascula genitalia. The genitalia have the same morphology as those in the pedicle valve. They cover broad flabellate areas on the lateral and postero-lateral parts of the valve, but have a smaller area than the genitalia on the pedicle valve because they are confined by the vascula myaria.

A system of narrow linear canals at the margins of mature shells (Pl. 74, figs. 1–3, 9; Pl. 75, figs. 1, 2) are continuous with small branching canals in the middle part of the shell (viz. the small canals between the vascula media in Pl. 74, fig. 3). These small branching canals are interpreted as impressions of a juvenile mantle canal system, and hence their distal parts are regarded as impressions of mantle canals, probably impressions of the termination of the canals at the proximal ends of the setal follicles. These impressions were apparently continuously recorded by a process of differential thickening at the margin. The linear canals are joined by branches of a superimposed mantle canal system (see below), indicating their function as a canal rather than the trace of a setal follicle. Had they been merely traces of setal follicles they would intercalate as new setae were introduced around the margin; when they increase, these canals branch (Pl. 74, fig. 3; Pl. 75, fig. 3).

Changes in the mantle canals. In the pedicle valve the main canals of vascula media extending in front of the muscle field can be divided into three intergrading morphological types (text-fig. 6):

- A. Canals convex outwards and widely separated.
- B. Canals straight and widely separated.
- C. Canals straight and close together.

It has been shown above that the A and B types of canals typify small- to medium-sized individuals and C type canals larger individuals, and hence the different shapes of the vascula media can be explained as stages in the ontogenetic development of the individual. Accompanying the change from the A to C types of canals is the enlargement of the complex network of the vascula genitalia, and it is suggested that this enlargement within the mesenchyme layer of the mantle gradually forced the vascula media canals together and the lateral canals to move towards the margin as the shell became older. Specimens having each of these types of canals are present in all of the horizons in the Gresford district.

This explanation of the development of the canals does not account for their distribution as outlined in Table 2, unless evolution has taken place.

An analysis of Table 2 is simplified if it is realized firstly that the C type canal is that seen in the largest specimens, and secondly that the L. 53 sample is dominated by large specimens (text-fig. 7). Table 2 shows a decrease in A type canals and an associated

increase in B type canals from the oldest to the youngest horizons. This trend could be explained in at least two ways: as the expression of the ontogeny, as outlined above, in which sampling errors gave the impression of a genetic change, or as a true genetic change towards the earlier maturity of the genitalia.

An examination of the width-frequency polygons (text-fig. 3) shows that the samples are essentially the same in terms of size distribution, except for L. 53. Also, the specimens from the highest stratigraphic horizon with B type canals are about the same size as specimens from the lower horizons characterized by A type canals. In the absence of genetic change the specimens having the B type canals should have been larger.

TABLE 2

	Canal types		
	A	B	C
L. 53 Greenhills	Occasional	30%	70%
L. 206 Lewinsbrook Syncline	25%	75%	occasional
L. 270 Trevallyn	65%	35%	occasional
L. 218 } Gresford Quarry	65%	35%	occasional
L. 50 }			
L. 215 Lewinsbrook	70%	30%	occasional

More conclusive evidence in favour of the genetic change is available from younger horizons (probably middle to upper Viséan) at Barrington, N.S.W., in which moderate to large specimens of *S. verulamensis* have mainly straight, sub-parallel (or B type) canals (Cvancara 1958).

The earlier maturity of the genitalia would have increased the number of larvae produced by each individual and probably significantly increased the *S. verulamensis* population to one of even greater dominance during the Viséan.

Superimposition of mantle canals. In mature specimens of *Schizophoria verulamensis*, particularly in pedicle valves, the greater part of the mantle canal system is superimposed over small radial canals. The small canals originate from the body cavity frequently branch, and run irregularly towards the front of the shell. In mature valves the posterior parts of these canals (viz. the narrow branching canals between the main vascula media in Pl. 74, fig. 3) are interpreted as the traces of juvenile mantle canals.

EXPLANATION OF PLATE 75

Schizophoria verulamensis Cvancara

Fig. 1. $\times 2$. F.7152a. Internal mould of pedicle valve showing narrow canals extending from the front of the muscle field and being truncated by the superimposed mature mantle canal system; L. 50 Gresford Quarry.

Fig. 2. $\times 2$. F.7146k. Internal mould of pedicle valve; L. 270 Trevallyn.

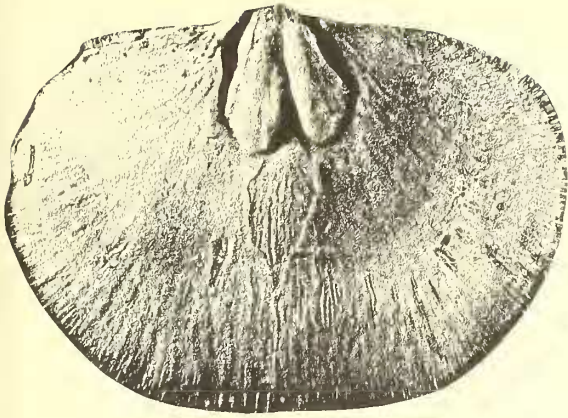
Fig. 3. $\times 2$. F.4677b. Internal mould of pedicle valve; L. 215 Lewinsbrook.

Fig. 4. $\times 1$. F.7144o. Internal mould of an old pedicle valve; L. 53 Greenhills.

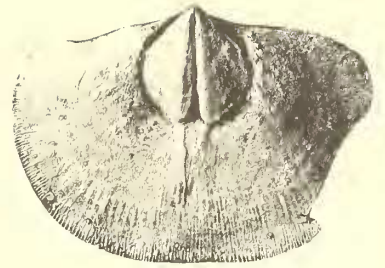
Fig. 5. $\times 1$. F.4784. Internal mould of an old pedicle valve with C-type vascula media and large areas of vascula genitalia; L. 53 Greenhills.

Fig. 6. $\times 1$. F.7145b. Internal mould of an old pedicle valve; L. 270 Trevallyn.

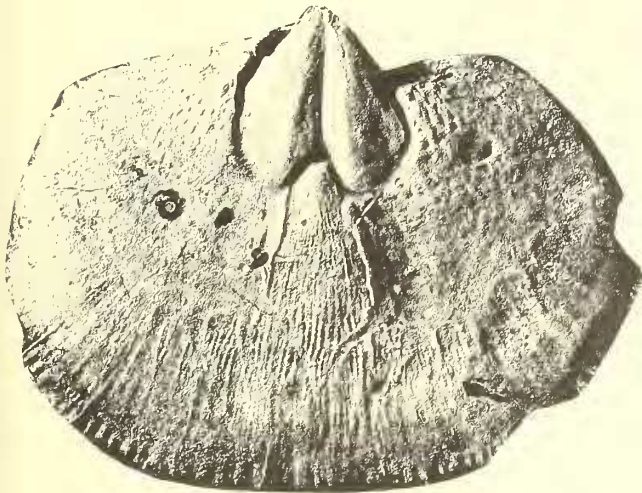
Fig. 7. $\times 1$. F.7146c. Internal mould of an old pedicle valve with large vascula genitalia, C-type vascula media and the lateral canals situated close to the margin; L. 270 Trevallyn.



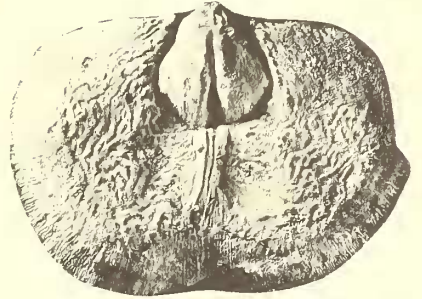
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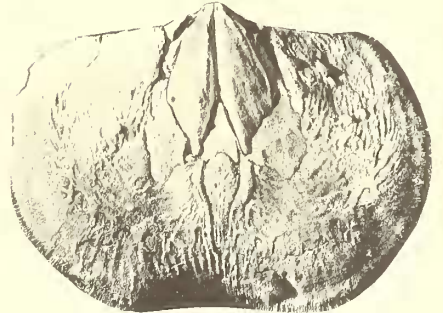
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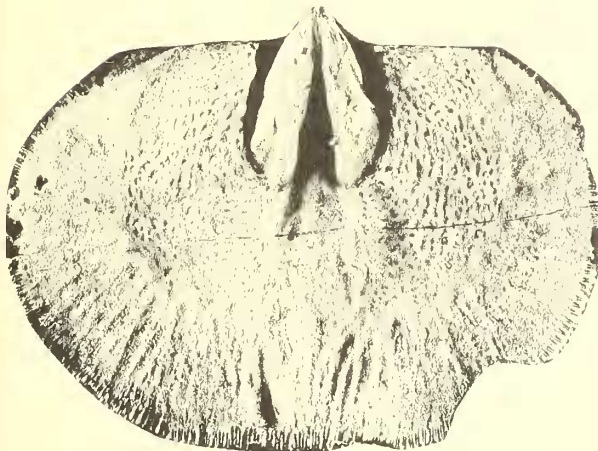
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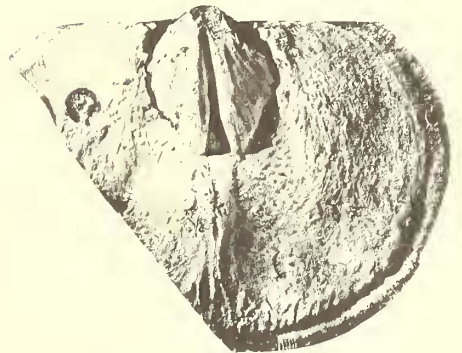
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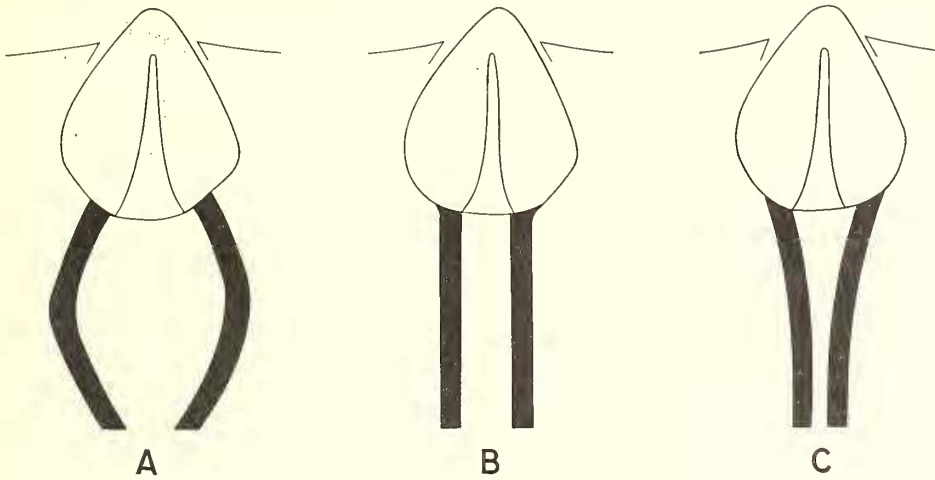
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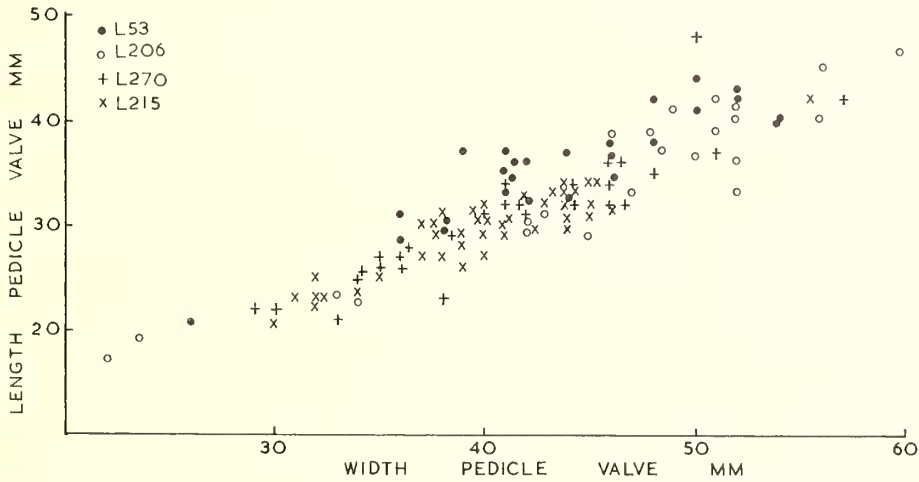
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Because all the canals were connected to the bases of the setal follicles (Williams and Rowell 1965) these juvenile canals are continuous with the traces, recorded at the margin, of the termination of the mantle canals at the setal follicles.



TEXT-FIG. 6. The three types of vascula media canals in the pedicle valve of *Schizophoria verulaensis* Cvcancara.



TEXT-FIG. 7. Scatter diagram of length plotted against width for pedicle valves of *Schizophoria verulaensis* Cvcancara from L. 215 Lewinsbrook, L. 270 Trevallyn, L. 206 Lewinsbrook Syncline, and L. 53 Greenhills.

In mature pedicle valves impressions of the small canals extend from the front of the muscle field between the large canals of vascula media, branching as they run towards the front of the valve (Pl. 74, fig. 3; Pl. 75, figs. 1, 2). In the middle and mid-anterior

parts of the valve they are truncated by superimposed larger canals: viz. the inner branch of the right-hand vasculum medium on the specimen in Plate 74, fig. 3 in which small canals extend on either side of a branch of the superimposed larger canal. Near the margins, the large canals join with the narrow linear traces left by the mantle canals at the ends of the setal follicles, and extend to the depressions left by the setal follicles. The junction between these canals results from both systems supplying the same setal follicles at the margin; the small linear marks were impressed as the shell grew, and the larger canals, which had been formed by the modification of the smaller ones, were impressed at a later time.

The superimposition of the mantle canal systems is less clear in the brachial valve. One large specimen, however, has a system of narrow linear canals beneath broad canals of *vascula media* (Pl. 74, fig. 9). The U-shaped branch on the left hand side of the *vascula media* truncates at least six of the narrow canals, and other narrow canals emerge from beneath the sites of bifurcation of the larger canals and are apparently continuous with the traces of the canals at the bases of the setal follicles.

The two main systems (i.e. the younger and older systems) described above are interpreted as impressions of the mantle canals at two different periods during the life of the shell, probable before and after sexual maturity. Because of the impression of a large or mature system on top of a smaller and probably immature system it is inferred that the major part of the canal system was impressed at certain well-spaced intervals instead of being continuously recorded on the inside of the shell.

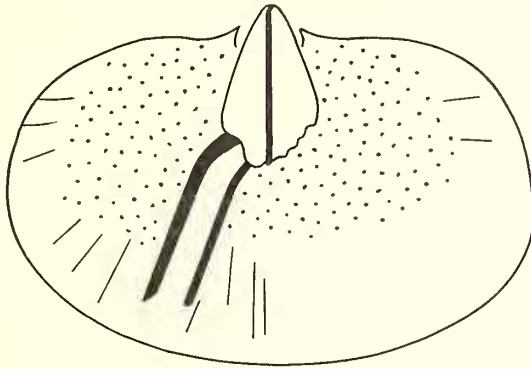
Williams (1956, p. 273) thought that mantle canals were impressed on the inner surface of the shell by differential secretion of shell material by the outer epithelium covering the canals. In *S. verulamensis* this mechanism may have been responsible for the continuous impression of the distal parts of the canals at the margin, but it could not have been responsible for the impression of the main part of the mantle canal system, because there are two and sometimes three systems superimposed over one another, unless rapid differential secretion took place at specific times; this is unlikely because it means that rather than being gradually thickened the shell would have been periodically rapidly thickened.

A more convincing explanation is that the outer epithelium over the mantle canals resorbed the shell material at specific times. Resorption is most likely to have taken place during the periods of limited shell growth when the mantle canal system had a stable morphology. During periods of rapid growth there would have been continuous reorganization of the mantle canals at the mantle edge and the development of additional setal follicles at the growing margin. To maintain efficient circulation to the margin the main canals of *vascula media* and *vascula myaria* would have enlarged by reorganizing the connective tissue in the mantle and coalescing with smaller canals. Many modern shallow-water marine organisms, particularly molluscs, cease depositing shell during the colder months of the year (Epstein and Lowenstam 1954), and hence it is reasonable to assume that the winter was the most likely time for the retardation of shell deposition and the impression of the mantle canals in *S. verulamensis*.

Abnormal mantle canals. In the pedicle valve figured in Plate 74, fig. 4, the left-hand canal of *vascula media* divides a short distance in front of the muscle field, giving a third main canal extending to the median anterior part of the valve. All three canals

branch in a similar manner to those in other valves. Functionally this additional large branch may have provided a greater supply of coelomic fluid to the growing edge of the front of the mantle. The two outer canals of *vascula media* give off arcuate lateral canals.

Another specimen showing an abnormal development of the *vascula media* (text-fig. 8) has impressions of the two main canals of *vascula media* arising from the anterior margin of the left diductor muscle scar and running, parallel with one another, to the antero-lateral part of the valve. There is no canal originating from near the right diductor scar, presumably because of some injury or functional defect to that side of the body cavity, and the *vascula genitalia* extend in front of the muscle scar. The



TEXT-FIG. 8. Pathological pedicle valve of *Schizophoria verulmensis* Cvancara showing the two main canals of *vascula media* extending from the left diductor muscle scar, and the *vascula genitalia* extending in front of the right diductor muscle scar.

preservation is too poor to trace the junction of the right-hand canal with the right lateral canal. This variation indicates a certain adaptability in the organization of the mesenchyme layer of the mantle, and supports the arguments put forward above that major reorganizations took place within the mantle during the development of the species. Other features probably associated with this deformity are a deep furrow on the antero-median part of the left diductor muscle scar and an exceptionally narrow median ridge which does not expand anteriorly.

In a large pedicle valve (Pl. 75, fig. 6) branches from the arcuate lateral canal in the posterior part of the valve, instead of extending normal to the margin of the valve, turn posteriorly and run almost parallel with the margins, diverging only slightly from the main lateral canal. In other valves (Pl. 74, fig. 3) only the posterior-most branches of the lateral canal turn and run more or less parallel with the canal.

Connexion between the mantle canals. The description and figures of mantle canals of fossil brachiopods given by Williams (1956) and Williams and Rowell (1965) suggest that each of the three pairs of extensions of the coelomic cavity into the mantle—the *vascula media*, *vascula myaria*, and *vascula genitalia*—is a discrete unit, unconnected with other canals.